

# Control Mechanisms in Developmental Processes

## Control Mechanisms in Developmental Processes The Twenty-Sixth Symposium The Society for Developmental Biology

(Formerly the Society for the Study of Development and Growth)

La Jolla, California, June 1967

### EXECUTIVE COMMITTEE 1966–1967

SAMUEL GRANICK, Rockefeller University, President
WINSLOW R. BRIGGS, Harvard University, Secretary
ALFRED J. COULOMBRE, National Institutes of Health, Treasurer
MAC V. Edds, Jr., Brown University, Editor-in-Chief
MICHAEL LOCKE, Symposium Editor, Case Western Reserve University
JOHN W. SAUNDERS, Jr., Marquette University
HOWARD A. SCHNEIDERMAN, Case Western Reserve University
JEROME A. SCHIFF, Brandeis University

# Control Mechanisms in Developmental Processes

## Edited by Michael Locke

Developmental Biology Center Case Western Reserve University Cleveland, Ohio

Developmental Biology, Supplement 1

Editor-in-Chief M. V. Edds, Jr.

#### 1967

ACADEMIC PRESS, New York and London

COPYRIGHT © 1968, BY ACADEMIC PRESS INC.

ALL RIGHTS RESERVED.

NO PART OF THIS BOOK MAY BE REPRODUCED IN ANY FORM, BY PHOTOSTAT, MICROFILM, OR ANY OTHER MEANS, WITHOUT WRITTEN PERMISSION FROM THE PUBLISHERS.

ACADEMIC PRESS INC. 111 Fifth Avenue, New York, New York 10003

United Kingdom Edition published by ACADEMIC PRESS INC. (LONDON) LTD. Berkeley Square House, London W.1

LIBRARY OF CONGRESS CATALOG CARD NUMBER: 55-10678

PRINTED IN THE UNITED STATES OF AMERICA

#### Contributors and Presiding Chairmen

Numbers in parentheses indicate the pages on which the authors' contributions begin.

- I. The Role of Cytoplasmic Units
- LAWRENCE BOGORAD, Department of Botany, University of Chicago, Chicago, Illinois (1)
  - Chairman: June Lascelles, University of California, Los Angeles, California
- E. L. TATUM AND D. J. L. LUCK, The Rockefeller University, New York, New York (32)
  - Chairman: Aharon Gibor, University of California, Santa Barbara, California
- SIR JOHN RANDALL, T. CAVALIER-SMITH, ANNE McVITTIE, J. R. WARR, AND J. M. HOPKINS, Department of Biophysics, University of London King's College, London, England (43)
  - Chairman: Hans H. Went, Washington State University, Pullman, Washington
- II. The Role of the Nucleus
- BARBARA McCLINTOCK, Genetics Research Unit, Carnegie Institution of Washington, Cold Spring Harbor, New York (84)
  - Chairman: Herbert Stern, University of California, San Diego, California
- G. Ledyard Stebbins, Department of Genetics, University of California, Davis, California (113)
  - Chairman: Ralph Erickson, University of Pennsylvania, Philadelphia, Pennsylvania
- Boris Ephrussi, Western Reserve University, Cleveland, Ohio, and Mary C. Weiss, New York University Medical Center, New York, New York (136)
  - Chairman: Clifford Grobstein, University of California, San Diego, California

#### CONTRIBUTORS AND PRESIDING CHAIRMEN

- Albert Tyler, Division of Biology, California Institute of Technology, Pasadena, California (170)
  - Chairman: Arthur H. Whiteley, University of Washington, Seattle, Washington

#### III. Regulatory Mechanisms

- IRVING M. LONDON, ANTHONY S. TAVILL, GRACE M. VANDERHOFF, ARTHUR I. GRAYZEL, Department of Medicine, Albert Einstein College of Medicine and Bronx Municipal Hospital Center, New York, and Timothy Hunt, Fellow, Clare College, Cambridge (227)
  - Chairman: F. H. Wilt, University of California, Berkeley, California
- ROBERT AUERBACH, Department of Zoology, University of Wisconsin, Madison, Wisconsin (254)
  - Chairman: Leonard Hertzenberg, Stanford Medical School, Palo Alto, California
- SHELDON J. SEGAL, The Population Council, The Rockefeller University, New York, New York (264)
  - Chairman: I. S. Edelman, University of California, San Francisco, California

#### Foreword

In 1939, N. J. Berrill introduced the first symposium of the Society with the words:

"Biologists are finding themselves increasingly perplexed by the lack of an adequate conceptual framework with which to guide their own investigations and to bring the results of many specialized studies into a more coherent and meaningful relationship.

"With this need in view, a Symposium on 'Development and Growth' sponsored by the Editors of 'Growth' was held at North Truro, Mass., from August 7th to 11th, 1939. Sessions were held each morning and afternoon, each beginning with a paper lasting about one hour and followed by unhurried discussion and comment."

Over the years the Society has striven to maintain an unhurried atmosphere at the meetings, in part by publishing the papers so that members can listen with the assurance that the printed word will soon assist their memories.

From this beginning the Society for Developmental Biology has emerged to represent the multidisciplined field originally covered by "Development and Growth." After a varied history we now once again have both a journal and an annual symposium volume. To cement the Society's association with its journal, *Developmental Biology*, yet more firmly, all future symposia will be published as annual supplements.

#### HISTORY OF THE SYMPOSIUM VOLUMES

| No. | Held          | Title  | Editor            | Publisher                   |
|-----|---------------|--|-------------------|-----------------------------|
| 1   | Aug. 1939     | Development and Growth                               | Editors of Growth | Supplement to Vol. 1, 1939  |
| 2   | June 1940     | Development and Growth                               | Editors of Growth | Supplement to Vol. 2, 1940  |
| 3   | July 1941     | Development and Growth                               | Editors of Growth | Supplement of Vol. 5, 1941  |
| 4   | Aug. 1942     | Development and Growth                               | Editors of Growth | Supplement of Vol. 6, 1942  |
| 5   | 0             | 1945 Not published                                   |                   |                             |
| 6   | Aug. 1946     | Perspectives in                                      | Editors of Growth | Supplement of Vol. 10, 1946 |
|     | 8             | Development and Growth                               |                   |                             |
| 7   | Aug. 1947     | Published as Volume 11, No. 4,                       | 1947, of Growth   |                             |
| 8   | Aug. 1948     | Development and Growth                               | Editors of Growth | Supplement of Vol. 12, 1948 |
| 9   | AugSept. 1949 | Development and Growth                               | Editors of Growth | Supplement of Vol. 13, 1949 |
| 10  | AugSept. 1951 | Development and Growth                               | Editors of Growth | Supplement to Vol. 15, 1951 |
| 11  | June 1952     | Dynamics of Growth Processes                         | E. J. Boell       | Princeton Univ. Press, 1954 |
| 12  | June 1953     | Biological Specificity and Growth                    | E. G. Butler      | Princeton Univ. Press, 1955 |
| 13  | June 1954     | Aspects of Synthesis<br>and Order in Growth          | Dorothea Rudnick  | Princeton Univ. Press, 1954 |
| 14  | June 1955     | Cellular Mechanisms in<br>Differentiation and Growth | Dorothea Rudnick  | Princeton Univ. Press, 1956 |
| 15  | July 1956.    | Rhythmic and Synthetic<br>Processes in Growth        | Dorothea Rudnick  | Princeton Univ. Press, 1957 |
| 16  | June 1957     | Developmental Cytology                               | Dorothea Rudnick  | Ronald Press, 1959          |
| 17  | June 1958     | Cell Organism and Milieu                             | Dorothea Rudnick  | Ronald Press, 1959          |
| 18  | June 1959     | Developing Cell Systems<br>and Their Control         | Dorothea Rudnick  | Ronald Press, 1960          |
| 19  | June 1960     | Synthesis of Molecular and<br>Cellular Structure     | Dorothea Rudnick  | Ronald Press, 1961          |

| 20 | June 1961 | Regeneration  | Dorothea Rudnick | Ronald Press, 1962   |
|----|-----------|---|------------------|----------------------|
| 21 | June 1962 | Cytodifferentiation and<br>Macromolecular Synthesis   | Michael Locke    | Academic Press, 1963 |
| 22 | June 1963 | Cellular Membranes in Development                     | Michael Locke    | Academic Press, 1964 |
| 23 | June 1964 | The Role of Chromosomes in Development                | Michael Locke    | Academic Press, 1964 |
| 24 | June 1965 | Reproduction: Molecular,<br>Subcellular, and Cellular | Michael Locke    | Academic Press, 1965 |
| 25 | June 1966 | Major Problems in<br>Developmental Biology            | Michael Locke    | Academic Press, 1966 |

#### Contents

| CONTRIBUTORS AND PRESIDING CHAIRMEN                         | v    |
|---|------|
| Foreword  | vii  |
| HISTORY OF THE SYMPOSIUM VOLUMES                            | viii |
|   |      |
|   |      |
| I. The Role of Cytoplasmic Units                            |      |
| Control Mechanisms in Plastid Development                   |      |
| LAWRENCE BOGORAD  |      |
| Introduction  | 1    |
| The Control of Plastid Development by the Nuclear Genome    | 5    |
| Proplastid to Chloroplast                                   | 7    |
| Summary Discussion  | 24   |
| Chairman's Comments—June Lascelles                          | 28   |
| References  | 29   |
| Nuclear and Cytoplasmic Control of Morphology in Neurospora |      |
| E. L. TATUM AND D. J. L. LUCK                               |      |
| Comparison of Biochemical and Morphological Mutants .       | 32   |
| Nuclear Control of Morphology                               | 32   |
| Extranuclear Control of Morphology                          | 33   |
| Involvement of Mitochondria                                 | 33   |
| Possible Involvement of Mitochondrial DNA                   | 34   |
| Cytology of Abnormal Cultures                               | 36   |
| Biology of Conversion                                       | 36   |
| Cytochrome Pattern in Conversion                            | 39   |
| Conclusions   | 40   |
| References  | 41   |

| CONTENTS | х |
|----------|---|
| CONTENTS | Х |

| Developmental and Control Processes in the Basal<br>Bodies and Flagella of <i>Chlamydomonas reinhardii</i> |                   |
|--|-------------------|
| Sir John Randall, T. Cavalier-Smith,<br>Anne McVittie, J. R. Warr, and J. M. Hopkins                       |                   |
| Introduction   | <b>4</b> 3        |
| Basal Bodies in <i>Chlamydomonas reinhardii</i> The Genetic Control of Flagella Structure in               | 48                |
| Chlamydomonas reinhardii   | 53                |
| Macromolecular Basis of Morphopoiesis and Structure in Flagella  | 58                |
| Structure in Flagella  | 00                |
| Experimental and Theoretical Considerations  | 60                |
| General Discussion   | 76                |
| References   | 81                |
| Genetic Systems Regulating Gene Expression during Development BARBARA McCLINTOCK                           |                   |
|  |                   |
| Introduction   | 84                |
| System in Maize  | 88                |
| Evidence of Controlling Elements in Organisms  | 105               |
| Other Than Maize   | 105<br>111        |
| References   | 111               |
| Gene Action, Mitotic Frequency, and Morphogenesis in Higher Plants   |                   |
| G. Ledyard Stebbins  |                   |
| Introduction   | 113<br>114<br>116 |

xii CONTENTS

| Developmental Features of Corngrass in Maize   |      |     |     |    | 117 |
|--|------|-----|-----|----|-----|
| The Hooded Gene in Barley  |      |     |     |    | 123 |
| Relationship between Mitotic Frequency and   |      |     |     |    |     |
| Orientation of Mitoses   |      |     |     |    | 126 |
| Discussion and Summary   |      |     |     |    | 131 |
| References   |      |     |     |    |     |
| Regulation of the Cell Cycle in Mammalian Cells<br>Inferences and Speculations Based on Obser<br>of Interspecific Somatic Hybrids                  |      | ion | s   |    |     |
| Boris Ephrussi and Mary C. Weiss   |      |     |     |    |     |
| Prefatory Note   |      |     |     |    | 136 |
| Introduction   |      |     |     |    | 137 |
| Properties of Rat X Mouse and Hamster X Mo   |      | Hy  | bri | ds | 139 |
| Inferences concerning the Coordination of the l  |      |     |     |    |     |
| of the Cell Cycle  |      |     |     |    | 146 |
| Appendix I: Summary of Work on Hybridization   | on ( | of  |     |    |     |
|  |      |     |     |    | 162 |
| Somatic Cells  |      |     |     |    | 163 |
| References   |      |     |     |    | 166 |
|  |      |     |     |    |     |
| Masked Messenger RNA and Cytoplasmic DNA in Relation to Protein Synthesis and Processe of Fertilization and Determination in Embryonic Development |      |     |     |    |     |
| Albert Tyler   |      |     |     |    |     |
| Introduction   |      |     |     |    | 170 |
| Introduction  Messenger RNA  Stimulation of Protein Synthesis upon Fertilization   |      |     |     |    | 171 |
| Stimulation of Protein Synthesis upon Fertilization  | on   |     |     |    | 173 |
| Evidence for Masked Messenger RNA (mmRNA   | (1   |     |     |    | 174 |
| Extent and Duration of Action of mmRNA .   |      |     |     |    | 179 |
| mmRNA Synthesis during Early Development   |      |     |     |    | 183 |
| Polysome Formation upon Fertilization  |      |     |     |    | 184 |
| Protein Synthesis in Unfertilized Eggs   |      |     |     |    | 184 |
| Location of mmRNA in Unfertilized Eggs and   | in   |     |     |    |     |
| Developing Embryos   |      |     |     |    | 192 |

| CONTENTS   | xiii                                       |
|--|--|
| Relation of Histones to mRNA Synthesis   | <br>197<br>199<br>202<br>211<br>212<br>214 |
| III. Regulatory Mechanisms   |  |
| Erythroid Cell Differentiation and the Synthesis and Assembly of Hemoglobin  IRVING M. LONDON, ANTHONY S. TAVILL, GRACE A.   |  |
| Vanderhoff, Timothy Hunt, and Arthur I. Grayzel  Introduction  | 227<br>229<br>236<br>239<br>242<br>249     |
| The Development of Immunocompetent Cells ROBERT AUERBACH   |  |
| Introduction  Tissue Interaction during Lymphoid Morphogenesis The Thymus as a Source of Immunocompetent Cells Bone Marrow as a Source of Immunocompetent Cells Embryonic Liver as a Source of Immunocompetent Cells Yolk Sac Origin of Immunocompetent Cells Concluding Remarks Addendum References | 258<br>259<br>260<br>260                   |
| Regulatory Action of Estrogenic Hormones SHELDON J. SEGAL  |  |
| Introduction   | 264<br>267                                 |

xiv CONTENTS

| The Effect of Metabolic Inhibitors .   |   |  |  | 271 |
|--|---|--|--|-----|
| The Biological Activity of Uterine RNA |   |  |  | 272 |
| Morphological Effects                  |   |  |  | 273 |
| Enzymatic Effects                      |   |  |  | 274 |
| Physiological Effects                  |   |  |  | 276 |
| Estrogen Binding and RNA Synthesis     |   |  |  |     |
| References                             |   |  |  |     |
| Author Index                           |   |  |  | 281 |
| Subject Index                          | • |  |  | 290 |

#### I. THE ROLE OF CYTOPLASMIC UNITS

#### Control Mechanisms in Plastid Development

LAWRENCE BOGORAD<sup>1</sup>

Department of Botany, University of Chicago, Chicago, Illinois

#### INTRODUCTION

The metabolic activity of the plastid which is of greatest significance to the organism as a whole is photosynthesis, including the capture of light energy, its conversion to electrochemical energy, and the storage of this energy in carbon bonds. Thus, the chloroplast does photochemistry, electron transport, and carbon metabolism in the course of carrying out its photosynthetic activities. Precisely what the plastid does strictly for its own development and maintenance is more difficult to define. This discussion will deal primarily with chemical changes during the development of plastids in leaves of higher plants.

When full-grown the saucer-shaped chloroplasts in leaves of higher plants are approximately 10  $\mu$  across and 5  $\mu$  thick. Within the limiting membrane of such a plastid in maize (Fig. 1) is the lamellar system including the grana, which are composed of stacks of vesicles. The grana are interconnected in a complex manner. Outside the grana is the "stroma" region. A number of different kinds of studies, including examination by the freeze-etching technique (Mühlethaler, 1966; Park and Branton, 1966) and by low angle X-ray diffraction (Menke, 1966), indicate that the lamellae are made up of subunits. Within the stroma are ribosomes as well as strands of DNA (for discussion see, e.g., Bogorad, 1967) and many kinds of molecules that are too small to see.

It can be shown in a most elementary way that the photosynthetic pigments, the chlorophylls, are localized in the lamellar structure of the chloroplasts. Plastids are osmotically sensitive and can be liberated from the cell in media containing 0.5 M sucrose; they can be purified by differential or gradient centrifugation; and they can be ruptured by

<sup>&</sup>lt;sup>1</sup> Present address: The Biological Laboratories, Harvard University, Cambridge, Massachusetts.